Movement Behaviour and Resource Tracking in the Pine Weevil *Hylobius abietis*

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Abstract

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The pine weevil *Hylobius abietis* (L.) (Coleoptera, Curculionidae) is, economically, the most important forest pest over large areas of Europe. The adults feed on the stem bark of newly planted conifer seedlings, causing severe damage and mortality. The aim of this thesis was to obtain knowledge about behaviours of the pine weevil associated with its feeding, which may be of use in designing measures to protect seedlings.

A field experiment showed that the pine weevils use both olfaction and vision to find conifer seedlings. Their response to the combination of odour and visual stimuli were additive. Visual stimuli were at least as important as odour in finding an undamaged conifer seedling.

Soil scarification, which usually exposes mineral soil, is widely used in Scandinavian forest regeneration. In a field experiment, half as many seedlings on mineral soil were attacked by weevils as on undisturbed humus. However, somewhat more weevils approached seedlings surrounded by mineral soil than by humus. It is concluded that the surrounding soil type strongly influences whether a pine weevil decides to feed on a seedling, and that this decision is taken in close proximity to the seedling.

Another field experiment showed that feeding was less common on mounds of sand than on flat sand surfaces, but that there was more feeding in sandy pits. This effect of sandy slopes is attributed to the observed difficulty for the weevils to climb these slopes.

Many insects spend a large proportion of their life inactive, hiding in shelters. The presence of shelters may, therefore, influence where insects feed. Laboratory experiments demonstrated that the pine weevils were highly attracted to shelters both above and below ground. Visual stimuli were for orientation towards shelters. Visual stimuli also increased the probability of an individual remaining for a long period in a shelter. The presence of wind increased the weevils' propensity to use shelters both above and below ground.

The results of this thesis highlight the importance of planting seedlings in mineral soil, preferably on mounds, and of avoiding planting locations where the weevils can use above or below ground shelters in the vicinity of seedlings.

Keywords: Host plant acceptance, host volatiles, mounding, olfactory orientation, pitfall trap, reforestation, seedling damage, soil type, underground feeding, visual orientation.

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Appendix

Papers I-IV

This thesis is based on the following papers, which in the text are referred to by the corresponding Roman numerals I-IV.

I. Björklund, N., Nordlander, G. & Bylund, H. Olfactory and visual stimuli used in orientation to conifer seedlings by the pine weevil *Hylobius abietis*. Manuscript.

II. Nordlander, G., Bylund, H. & Björklund, N. Soil type and ground topography influencing feeding above and below ground by the pine weevil *Hylobius abietis*. Manuscript.

III. Björklund, N., Nordlander, G. & Bylund, H. (2003) Host-plant acceptance on mineral soil and humus by the pine weevil *Hylobius abietis* (L.). *Agricultural and Forest Entomology*, **5**, 61-65.

IV. Björklund, N. Cues for shelter use in a phytophagous insect. Manuscript.

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Introduction

Feeding is essential for survival and reproductive success, but how do insects find their food and what factors influence their feeding? The mechanical model of Miller & Strickler (1984) illustrates the relationship between the influences of external and internal factors (Fig. 1). The influence on behaviour of external factors, such as odour and visual stimuli, may differ depending on internal factors such as reproductive status, time since last meal, *etc*. (Barton Browne, 1993). It is convenient to divide the behavioural events leading to feeding in a phytophagous insect into three sequential steps: finding food, examining food, and consuming food (Fig. 1). Proceeding through this sequence, the number of sensory modalities that can be used increases, as does the strength of the stimuli. However, the sequence may be interrupted at any time if the "seesaw" tip over to the other side, as illustrated in Figure 1.

Papers I and III in this thesis deal with the finding step, or more precisely, with the influence of non-contact plant cues on the likelihood that individual conifer seedlings will be found by adults of the pine weevil *Hylobius abietis* (L.) (Coleoptera, Curculionidae). In Paper III, the number of weevils that found a seedling, *i.e.* completed the finding step, was compared to the number of weevils that proceeded through the whole sequence of steps, resulting in food consumption. This comparison was conducted both on humus and mineral soil to determine whether the differences in attack rates on the different soil types were due to differences during the finding step. In Paper II, the end result when the whole sequence of steps had been performed was measured and one factor, namely the difficulty in ascending sandy slopes, which influenced the finding step, was observed. Paper IV examined the finding step and the end result, but with respect to another resource, namely shelter.

The pine weevil

The pine weevil *H. abietis* feeds on the tender bark of several tree species but it prefers conifers (Leather *et al.*, 1994; Manlove *et al.*, 1997). Feeding occurs both in the crowns of mature trees (Örlander *et al.*, 2000) and on roots underground (Nordlander *et al.*, 2000). Larval development takes place in the roots of freshly killed conifers, and adult weevils migrate long distances (often more than 10 km) by flight to new breeding habitats during late spring (Solbreck, 1980). Fresh clear-cuttings in conifer forest stands provide abundant breeding substrate, and the pine weevil population density after immigration in spring has been estimated to be 14,000 weevils ha $^{-1}$ (Nordlander *et al.*, 2003a). After migration the pine weevil's flight muscles degenerate and the weevils remain on the ground for the rest of the season (Långström, 1982; Nordenhem, 1989; Örlander *et al.*, 1997; Örlander *et al.*, 2000). As a result of the longevity of pine weevils and the emergence of the new generation, a dense weevil population can persist within a clear-cutting for 4 years (Nordenhem, 1989; Örlander *et al.*, 1997). The pine weevil is an economically important pest since the adults feed on the stem bark of conifer seedlings (Day *et al.*, 2004; Day & Leather, 1997; Långström & Day, 2004).

However, planted conifer seedlings constitute only a fraction of the weevils' food requirement (Bylund *et al.*, 2004).

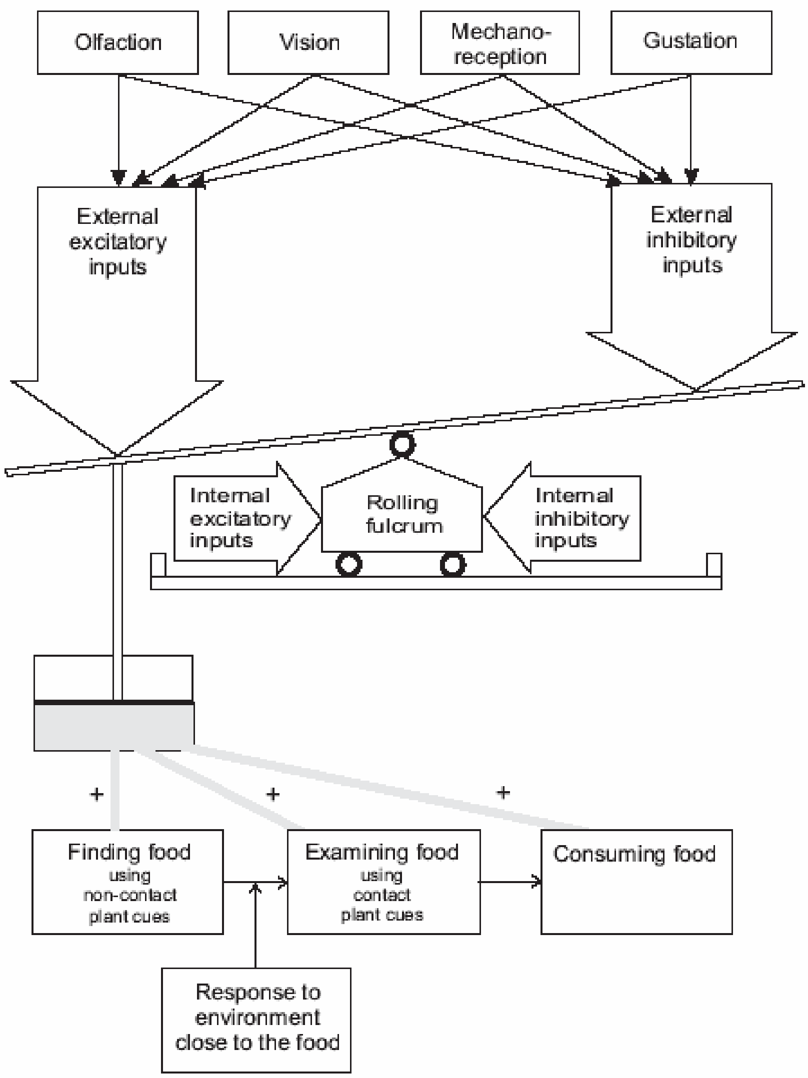

Figure 1 The influence of external and internal factors on the behavioural events leading an insect to feed. This is a modified version of Miller & Strickler's (1984) mechanical analogue of Dethier's (1982) model. It is suggested that the environment close to the food influences the sequence after the food is found.

Aims

The aim of this thesis was to obtain knowledge about behaviours of the pine weevil associated with its feeding, which may be of use in designing measures to protect seedlings. Three main questions were addressed:

How do the pine weevils find the conifer seedlings?

Baited traps emitting very high concentrations of conifer odour often catch large numbers of pine weevils. This does not, however, prove the significance of odour in finding individual conifer seedlings, which emit relatively little odour. Further, it is not known whether visual stimuli are used for finding individual seedlings. Field experiments were conducted to answer the following questions regarding how pine weevils find seedlings.

1) Do the pine weevils use odour emitted by the seedling? (Paper I)
2) Do the pine weevils use the visual appearance of the seedling? (Paper I)
3) Is there any interaction between odour and visual stimuli? (Paper I)
4) Is the higher rate of attack on wounded seedlings, which emits more odour, due to that more weevils find these seedlings? (Paper III)

Do properties of the ground surrounding a food source influence feeding?

Soil scarification is a widely used method in Scandinavian forest regeneration to obtain a favourable environment for conifer seedlings and to reduce damage caused by the pine weevil. Scarification breaks up the humus surface and often exposes mineral soil. However, it is not fully understood why mineral soil around conifer seedlings reduces the amount of feeding damage caused by the pine weevil. The following questions were considered.

1) Does the ground topography around the food source influence feeding? (Paper II)
2) Do the pine weevils prefer to feed above or below ground, and does the surrounding soil type influence the feeding position? (Paper II)
3) Does the mineral soil influence the rate of attack in some other way than through its influence on the condition of the seedling? (Paper III)
4) Are the pine weevils less responsive to plant odour when they are moving rapidly, as they do on mineral soil? (Paper III)
5) Is the damage-reducing effect of mineral soil due to fewer weevils arriving at seedlings planted in mineral soil than similar seedlings in humus? (Paper III)

Are shelters attractive and what factors influence shelter use?

The presence of shelter may influence the amount of time insects spend within a given area and hence where they feed. There are fewer shelters on mineral soil than on humus, and the pine weevil is more inclined to burrow in humus. Accumulation of litter and ingrowth of vegetation, which may be used as shelters, on soil scarified areas increase pine weevil damage. In order to increase our understanding of the use of shelters, the following questions were considered.

1) Are shelters attractive to the pine weevils? (Paper IV)
2) Do visual stimuli affect the probability that a shelter is used? (Paper IV)

3) Do visual stimuli affect the time that pine weevils remain within shelters? (Paper IV)
4) Does wind affects the weevils' propensity to use above or below ground shelters? (Paper IV)

Materials

Pitfall traps

In order to measure the number of weevils approaching a stimulus, *e.g.* a conifer seedling, a new type of pitfall trap was developed (Fig. 2). The pitfall trap had to fulfil several criteria: 1) it should hold enough water to supply a seedling for one week; 2) it had to be constructed without glue to avoid any extraneous odours; and 3) it should catch the weevils as close as possible to the seedling. During the development of the pitfall trap I found that a large proportion of the weevils were able to grip the rim of a standard pitfall trap with the claws of their hind legs and thereby avoid being trapped (Fig. 2). The pitfall traps were therefore equipped with a sloping rim (Fig. 2).

In studies on the closely related *Hylobius pales* (Herbst) a trap consisting of a 0.6-m square made from gutter pipe placed around the seedlings has been used to measure the number of approaching weevils (Hertel, 1970; Thomas & Hertel, 1979). These authors caught similar numbers of weevils in traps surrounding seedlings as in the controls. However, this may be because the weevils were caught outside the area in which stimuli from the seedlings could have induced a response. The new type of pitfall trap that we developed trapped approaching *H. abietis* individuals 2.5-cm from the seedling; approximately twice as many weevils were caught in pitfall traps with seedlings compared to the controls (Papers I and III).

Results and discussion

Olfactory and visual stimuli used in orientation to conifer seedlings (Paper I)

How do the pine weevils find the conifer seedlings?

In a field experiment the influence of non-contact plant cues was determined by capturing pine weevils in traps when they approached different combinations of olfactory and visual stimuli (*cf.* Fig. 1). Since conifer seedlings emit odour, dummy-seedlings were used to provide a solely visual stimulus. Odour was produced by buried stem sections of conifer seedlings.

Large numbers of weevils were caught in traps with conifer seedlings in fresh, one-year-old, and two-year-old clear-cuttings, which suggests that almost all seedlings in a clear-cutting are likely to be encountered by pine weevils (Papers I and III). In support of this, a later study showed that almost all plant groups in a clear-cutting are likely to be encountered by weevils during a single season (Nordlander *et al.*, 2003a). However, since many fewer seedlings were attacked than encountered (Paper III), pine weevils must often encounter seedlings without feeding on them. Whether they will feed or not should be influenced by internal factors (position of the rolling fulcrum in Fig. 1) such as time since the last meal etc. (Barton Browne, 1993). Thus, the number of pine weevils arriving should influence the probability of a seedling being attacked.

Both pine odour alone and visual stimulus alone increased the number of approaching pine weevils. When both odour and visual stimulus were provided the response was additive, *i.e.* the response to the combination of stimuli was as strong as the sum of the individual stimuli. Visual stimulus appears to be at least as important as odour to weevils for finding an undamaged conifer seedling, since approximately half as many weevils were caught around odourless dummy-seedlings as around real undamaged seedlings.

Figure 2 Pitfall trap used in Papers I and II (below left), components used to construct it (upper) and a pine weevil gripping the rim of a standard pitfall trap (below right).

Age and reproductive status have been shown to influence responses to non-contact odour and visual stimuli in other insects (Barata & Araújo, 2001; Borden et al., 1986; Brevault & Quilici, 1999; Hoffman et al., 1997; Landon et al., 1997; Mathieu et al., 2001; Prokopy, 1977). However, reproductive status or age of the weevils (position of the rolling fulcrum in Figure 1) did not effect the pine weevils' response to odour and visual stimuli from conifer seedlings. Neither was there any effect of season or age of the clear-cutting (strength of external stimuli in Figure 1).

Soil type and ground topography influencing feeding above and below ground (Paper II)

Do the ground topography and soil substrate around the food influence feeding?

Soil scarification creates a good environment for conifer seedlings establishment and growth (Örlander *et al.*, 1990) and decreases the damage caused by the pine weevils (Lindström *et al.*, 1986; von Sydow, 1997; Thorsén *et al.*, 2001; Örlander & Nilsson, 1999). Pits or mounds can be created as part of the soil scarification process. Planting in mounds generally results in low levels of weevil damage (Söderström *et al.*, 1978; Örlander *et al.*, 1990; Örlander & Nilsson, 1999), whereas seedlings planted in pits are subject to more damage than those on mounds (Örlander *et al.*, 1990). In Paper II the amount of consumption was measured on stem sections inserted vertically into the ground in areas of sand with different topographies (flat, mound, and pit) and in flat areas with fine-grained humus.

Less pine bark was consumed from stem sections on mounds of sand than on flat sand surfaces. Although the pine weevil has a very good attachment mechanism that enables it to walk upside down on smooth surfaces (personal observation), they were observed to have difficulty walking on a slope of sand with an inclination of only 27°. This is because the weevils slip when grains of sand come loose. Ground beetles display considerable differences, according to species, in their abilities to walk on slopes of sand without falling (Andersen, 1978). Most feeding occurred in pits, probably because the weevils got trapped there.

Planting conifer seedlings on mounds or in pits also influences the condition of the seedlings (Örlander *et al.*, 1990), but in the present study the stem sections was replaced frequently to minimise the influence on food quality. The large effect of the different topographies on feeding indicates that this is an important factor even without its influence on the seedling itself.

Do the pine weevils prefer to feed above or below ground? Almost all feeding occurred below ground both on fine-grained cultivated humus and on mineral soil. The high level of feeding underground, in combination with the pine weevil's ability to locate roots when walking on the ground and burrow down to them (Nordlander *et al.*, 1986), supports the suggestion that conifer roots are an important food source (Nordlander *et al.*, 2003a; Nordlander *et al.*, 2003b).

Host-plant acceptance on mineral soil and humus (Paper III)

Is the higher rate of attack on wounded seedlings, which emits more odour, due to that more weevils find these seedlings? In Paper III and in an earlier study (Nordlander, 1991) mechanically wounded conifer seedlings were attacked three to five times as often as seedlings without wounds. However, in Paper III it was shown that an increased odour emission only slightly increased the number of *approaching* pine weevils. This suggests that the increased risk of attack to wounded seedlings is mainly due to factors that influence behaviour during the examining or consumption steps (*cf.* Fig. 1). One such factor may be a weakened defence system in wounded seedlings (Långström & Day, 2004). There was no support for our hypothesis that pine weevils do not respond to plant odour when moving rapidly, as they do on mineral soil (Kindvall *et al.*, 2000).

Does mineral soil influence the rate of attack in some other way than through its influence on the condition of the seedling? Several earlier studies have investigated the effect of mineral soil on pine weevil damage. In these studies soil scarification methods exposing a rather deep layer of mineral soil that creates a good environment for the seedling has been used (Lindström *et al.*, 1986; Petersson *et al.*, 2004; von Sydow, 1997; Thorsén *et al.*, 2001; Örlander *et al.*, 1990; Örlander & Nilsson, 1999). It has therefore not been possible to determine whether the effect of the mineral soil is due to its influence on the condition of the seedling or to some other effect. However, in Paper III the influence of mineral soil on the condition of the seedling was minimised by adding mineral soil in as thin a layer as possible while still completely covering the ground. This treatment halved the number of attacks compared to seedlings in humus, which reveals that the mineral soil decreases the frequency of attacks, regardless of its influence on the condition of the seedling.

Is the damage-reducing effect of mineral soil due to fewer weevils arriving at conifer seedlings planted in mineral soil than similar seedlings in humus? Approximately the same number of pine weevils approached seedlings on mineral soil as on humus. We therefore suggest the protective effect of mineral soil is the result of fewer weevils remaining in the vicinity of seedlings in mineral soil. Mineral soil provides no shelters above ground and pine weevils are more inclined to burrow in humus than in sand (Paper II). The pine weevil is highly attracted to shelters both above and below ground (Paper IV). Thus, pine weevils may stay in the close vicinity of the seedling when potential shelters are provided, thus influencing the attack frequency (*cf.* Fig. 1).

Cues for shelter use (Paper IV)

Are shelters attractive and what factors influence shelter use?

It was shown that below-ground shelters were most attractive to weevils but above-ground shelters were also used more frequently than control zones. Visual stimuli from above ground shelters were used for orientation towards the shelters, and it was also shown that visual stimuli increase the time that pine weevils remain within a shelter. This appears to be the first study demonstrating that visual cues *per se* influence the use of shelters by an insect. Similar results have, however, been obtained for Crustaceans (Christiansen, 1971; Steele *et al.*, 1997).

Wind may affect the use of shelters such as ground vegetation, stones, crevices *etc*., but little is known about this. In Paper IV it was shown that wind increases the weevils' propensity to use shelters. This was the case for shelters both above and below ground. One of the few other studies that has investigated this showed that, for the Colorado potato beetle, there is a positive correlation between wind speed and hiding in weeds (Jermy *et al.*, 1988). Wind may be an underestimated factor influencing the spatial distribution of insects walking on the ground, *e.g.* wind may cause pine weevils to leave open windy areas that have no opportunities for shelter.

Management implications

Conifer seedlings should preferentially be planted in mineral soil and planting should be avoided not only in undisturbed humus (Lindström *et al.*, 1986; Petersson *et al.*, 2004; von Sydow, 1997; Thorsén *et al.*, 2001; Örlander & Nilsson, 1999) but also in cultivated humus (Paper II; Petersson *et al.*, 2004). Due to the pine weevil's difficulties in walking on sandy slopes with an inclination of only 27° it should be advantageous to plant on mounds and to avoid planting in pits or furrows, where weevils might get trapped. The high proportion of feeding underground suggests that conifer seedlings planted with the lower part of the stem below ground (deep planting) run a higher risk of pine weevil damage.

Attention should also be paid to minimising shelter possibilities for the pine weevils in the close proximity to seedlings, both in the development of soil scarification methods and when a spot is selected for planting each conifer seedling. Planting should also be avoided in depressions where accumulation of litter occurs and in substrates suitable for burrowing (*i.e.* humus). This may also be relevant for other systems where phytophagous insects cause damage to useful plants.

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